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BOTANICAL GAZETTE

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THE ALTERNATION OF GENERATIONS AND THE MORPHOLOGY OF THE SPORE FORMS IN THE RUSTS

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(WITH PLATE VII)

DEBARY (8) was the first to establish the doctrine of heteroecism and explain the relationships between the fructifications occurring in a complete life-cycle of a rust having all of the spore forms. He first proved by inoculation experiments that sporidia from teleuto-spores of *Puccinia graminis* Pers. when sown on the barberry produce there the spermagonia and aecidia, and further that these aecidio-spores taken from the barberry will again produce infections upon wheat.

In case of rusts which do not show a complete series of these spore forms it has been supposed and is still assumed to some extent that the missing stages exist, but are simply unknown in their correct relation to the known spore forms. But the methods of cross-infection, first successfully used by DEBARY (8, 9), have led to the solution of many of the problems so far worked out in the life-cycle of the rusts, and by suitable infection experiments it has been established that one or more of the spore stages found in rusts with a complete life-cycle of the *P. graminis* type are regularly lacking in certain other rusts.

The question of the nature of the life-history in the *-opsis*, *brachy-*, *hemi-*, *lepto-*, and *micro-* forms, with their abbreviated cycles, has become of special importance since the discovery of sexuality and alternation of generations in the rusts. When comparing the com-

plete life-cycle of a form like *Phragmidium violaceum* with that of *Phragmidium potentillae canadensis*, in which the aecidium is lacking, the question at once arises whether forms with a less number of spore types are to be considered as primitive and incomplete and in the process of developing into the conditions in *Eupuccinia*, or whether they are reduced and degenerate types. This question can be settled only on the basis of a complete morphological analysis of all the spore forms in question, and the following studies were undertaken as a contribution toward this end.

The most varied morphological interpretations have been given for each of the spore forms of the rusts, and it is worth while to summarize briefly the literature from this standpoint.

DEBARY'S (10) interpretation of the relations of the spore forms, given more than twenty years ago, has been recognized by many even to the present day as authoritative. He says: "The development of the aecidium-forming Uredineae agrees so nearly with that of the typical ascomycetes that certain stages in each group may be regarded as homologous with one another, though it must be allowed that the proof of the homologies is not quite perfect." The description of the formation of the aecidium cup is given somewhat as follows: The earliest stages consist of a tangled weft of hyphae. These enlarge, forming a dense mass which has the appearance of pseudo-parenchyma. This mass corresponds very well to the peritheium of certain ascomycetes. The hymenial cells appear at the base of this mass. From these club-shaped "basidia" the spores are abstricted to form rows. In his theoretical discussion DEBARY suggests the possibility of the hymenial layer having its origin in some large central female organ at the base of the aecidium. He was unable, however, to harmonize this view with what was known of the caeoma type of the aecidium.

In 1888, MASSEE (18) figured and described a peculiar organ occurring in the aecidium of *Uromyces poae* Rab. He made sections of the infected leaves of *Ranunculus ficaria*, and these sections were kept alive and studied as the processes went on. MASSEE found a large club-shaped branch at the base of the future pustule. A smaller antheridial cell was formed near by and fused with this oogonium, but the union was not clearly made out. The antheridium became

empty and dwindled, while the oogonium became large and dense and nodules budded out upon its surface. These nodules elongated and formed the "basidia" from which the rows of aecidiospores are abstracted. Those nodules formed near the base of the oogonium produced the peridium. Before the fusion he finds in the oogonium, on staining with methyl green, a well-defined nucleus. After the union with the antheridium, MASSEE observed several small nuclei in this organ. As to the nuclei of the nodules he gives us no data. This account of the origin of the aecidium would lead naturally to the conclusion that the aecidium cup is a unit structure arising from a single fertilization. In that respect it would be perfectly comparable to the ascocarp.

ROSEN (23) in 1892 gave quite a different account of the formation of the aecidium in the case of *Uromyces pisi* Pers. In this form the end cells of the hyphae which bear the spores become much enlarged and at first contain one nucleus. This divides and the two so formed lie in the vertical axis of the cell. The one nearer the apex of this "basidium" divides to form two, and the portion of the cell containing them is separated off by the formation of a wall. This leaves the "basidium" containing one nucleus and the process may be repeated. ROSEN gives no account of a central organ from which the hyphae bearing the "basidia" arise. In the absence of such an organ the argument that the cup is the unit structure loses force. This would be even more markedly true if the same account of spore formation were found true for the aecidia of the caeoma type.

A year later DANGEARD and SAPPIN-TROUFFY (7) published an account of work done on the aecidia and also the teleutospores of various rusts. They interpret the fusion of the nuclei occurring in the teleutospore as being a fertilization and give to the process the name *pseudofécondation*. They regard the mature teleutospore as a fertilized egg and attach little significance to the origin of the binucleated condition. SAPPIN-TROUFFY also made some observations upon the spore-formation in other stages of the rusts. In the teleuto pustules of *Gymnosporangium sabinae* he found that one of the two nuclei of the "hymenial cell" enters the bud. A wall separates the bud from the basal cell, after which the single nucleus divides. These two nuclei now lie side by side in the bud

and a simultaneous division occurs. A cell wall is then formed which separates the top or spore cell from the pedicel. SAPPIN-TROUFFY (25) later describes a similar budding in the uredospore pustule of *Uromyces betae* Pers. The process is the same except that a conjugate division of the two nuclei in the basal cell provides two nuclei for the young bud, instead of the basal cell sending one of its two nuclei into the bud. In my opinion it is altogether likely that the nuclear behavior in *Gymnosporangium sabinae* is the same as that described for *Uromyces betae*. In connection with his account of *Uromyces betae*, SAPPIN-TROUFFY points out the morphological likeness between the intercalary cell of the aecidium and the stalk cells of the uredospores. SAPPIN-TROUFFY (25) also shows that the cell at the base of the row of aecidiospores remains binucleated during spore-formation. The nuclear phenomena found in *Uromyces erythronii* DC. are different from those described by ROSEN. The two nuclei which normally lie irregularly placed in the end cell of the "sporiferous filament" come to lie side by side just before division. Simultaneous division of the two nuclei provides two nuclei for the cell which is to be separated off and leaves two to remain in the end cell of the hypha. SAPPIN-TROUFFY finds that in a great many rusts the binucleated phase has its beginning in these end cells. In his account there is no mention made of a large central organ such as was described by MASSEE. His observations, like ROSEN's, would indicate that the rows of spores are perfectly independent structures.

POIRIAULT and RACIBORSKI (21) gave a similar account of the behavior of the cells at the base of the aecidium. They believe that a single spindle is formed in the process of conjugate division, and with the work of SAPPIN-TROUFFY mentioned above have established quite satisfactorily that the two nuclei of the cells of the uredo and teleuto stages have each a distinct line of ancestors dating back to the basal cell of the aecidium at least.

In 1896 RICHARDS (22), working on *Uromyces caladii* Farl., found a large hypha, which he called the fertile hypha, at the base of the young aecidium. This hypha gives rise to several short branches, on the ends of which are borne the rows of spores. The "basidium," as he calls the end cell of one of these short branches, contains two or more nuclei; one migrates to the apex and there divides. The

portion of the "basidium" which contains the two nuclei is separated off by a wall. RICHARDS' observations on nuclear behavior are of rather uncertain value, since he believed that all parts of the aecidium, including the vegetative mycelium, contained binucleated cells. He describes the same general method of aecidium-formation for the aecidia on *Houstonia caerulea* and *Ranunculus septentrionalis*. The process here described shows a marked resemblance to that found by MASSEE. There is a large hypha, which may be the outgrowth from a sexual cell or may have so originated in the ancestors of the rust.

MAIRE (16), in 1900, found in *Endophyllum sempervivi* Alb. & Schw. that the vegetative hyphae consist of uninucleated cells to their very ends in the base of the aecidium. These end cells, however, enlarge and become binucleated by a nuclear division unaccompanied by a cell division. Upon this binucleated end cell the spores are borne. MAIRE holds this process to be quite universal in the aecidium. In another paper (17) published about the same time, MAIRE compares the life-history in the Uredineae with that of the mosses and ferns and of cyclops. He sees in the beginning of this binucleated phase in the life-cycle the change from gametophyte to sporophyte, and in the fusion of the nuclei in the teleutospore a "mixie," while in the germination of the teleutospore and in the promycelium there occur the reduction divisions. The doctrine of alternation of generations in the development of the rusts, while opposed in essential points to the views of DANGEARD and SAPPIN-TROUFFY, has found confirmation in the later work of BLACKMAN and myself.

BLACKMAN (2) in 1904 was perhaps the first to show that two cells are concerned in the production of the binucleated cell at the base of the row of aecidiospores. In *Phragmidium violaceum* Wint. he found a series of large uninucleated cells standing vertically beneath the epidermis of the host. Each cell cuts off a sterile apical cell and then becomes binucleated by the entrance of a nucleus from one of the neighboring vegetative cells. This nuclear migration is accomplished by the smaller nucleus from the vegetative cell penetrating the wall by drawing itself through a small perforation. BLACKMAN terms this cell containing the two nuclei the fertile cell, and from it the row of spores and intercalary cells is produced. BLACKMAN agrees with

MAIRE in his general conclusions regarding the chromatin fusion and reduction in the maturing and germination of the teleutospore. He further believes that the entrance of the vegetative nucleus is to be interpreted as a fertilization, though describing it as a "reduced fertilization" which has replaced a former fertilization by a true male cell—the spermatium.

Shortly after the appearance of BLACKMAN's paper, I described (5) a true fertilization in a somewhat similar form—*Phragmidium speciosum* Fr. The method of union of the two cells was found to be decidedly different. The cells combining are of approximately equal size, as are also their nuclei. Two such cells come together at some point on their adjacent walls. A considerable portion of the walls in contact dissolves away and the two protoplasts fuse. This large structure now elongates and from its apex a row of spores is abstricted (fig. 18). The same general behavior of the cells was found to occur in the aecidium of *Uromyces caladii*. Here, however, the cell produced by the fusion of the gametes elongates to a greater extent than in *Phragmidium speciosum*, and the two nuclei wander out into the elongated portion and remain there during spore-formation. The two bases of the gametes are often nearly obliterated. On the basis of these facts it was suggested that the rusts were after all more closely related to the lower fungi than to the red algae and ascomycetes. Certainly the union of the two cells is very like the zygospore formation common in the lower forms.

BLACKMAN and FRASER (3) in 1906 confirmed BLACKMAN's previous observations on nuclear migration, this time working on the aecidium of *Uromyces poae* Rab. As described for *Phrag. violaceum*, they found that the nucleus migrates through the cell wall. Similar migrations were found in the aecidium of *Puccinia poarum* Niels.

In the aecidium of *Melampsora Rostripi* Wagn., distinct evidences were obtained of the fusion of two large equal cells. In *Puccinia malvacearum* Mont., *Puccinia adoxae* DC., *Uromyces scillarum* Wint., and *Uromyces ficariae* Lév., BLACKMAN was unable to locate the origin of the binucleated phase. He suggests that a nuclear migration occurs in the hyphae some time between the infection with sporidia and aecidiospore-formation.

Still later (1907) I have described (6) a fusion of cells similar to

that previously described for *Phrag. speciosum* and *Uromyces caladii*, but occurring in the formation of the primary uredospores of *Phrag. potentillae canadensis* Fr. The conditions here resemble those in *Uromyces caladii* more closely in that the nuclei leave the bases of the original gametes and come to lie in a very much elongated outgrowth of the fusion cell (fig. 19). The first cell is separated off from this basal cell much as it is in the typical aecidium. This cell divides into a spore and into the smaller sterile cell, in the aecidium known as the intercalary cell. Here this sterile cell elongates to form a stalk upon which the spore is borne. A second spore and stalk are formed beside the first by the pushing-out of a bud which is separated from the basal cell by a wall. This cell is formed into a spore and stalk cell in the same manner as was the first. These observations confirm most positively WINTER'S (27) suspicion that the primary uredo represents the aecidium of the *Brachypuccinia* forms and suggest further the morphological likeness between the stalked spores and those which are borne in rows and are separated by intercalary cells.

The earlier writers were plainly of the opinion that the aecidium cup had its origin in a single sexual organ, in which case apparent homologies between the aecidium cup and the ascocarp were conceivable. The existence of a fusion at the base of a cup from which the spore-bearing hyphae arise is still not established. Even if established it would leave the development of the caeomas unexplained. All later work has shown the rows of spores to be independent of one another in their development, both in the caeomas and in the cuplike aecidia. There can be no question that there is an apparent morphological equivalence between a row of spores of the caeoma and a row of spores in the aecidium cup. That being the case, it would appear that the latter is simply a more compact and protected condition inclosed within the peridium. It is plain that this peridium is not to be compared with the perithecial wall of the ascocarp, since the latter is purely gametophytic, being an outgrowth from those hyphae which bear the gametes. The peridium of the aecidium cup is well known to consist of rows of abortive spores and hence is sporophytic. The sterile mass of cells, which DEBARY compares with the peritheciun and which appears before the hymenium is laid down, is perhaps comparable to the sterile cells which are cut from the gametes in

the caeomas just before the conjugation. From the closely built structure of the aecidium cup it would not necessarily follow that the structure is developed from a single organ, since we have uredospore pustules in the Coleosporiums, which, without having a peridium, are quite as compact as are the aecidium cups of such a form as *Uromyces caladii*, and no sexual process can be assumed to have occurred in their origin.

As a foundation for a correct morphological interpretation of these various spore forms, I have undertaken a careful study of the development of those spore types which do not originate in a fusion cell.

UREDOSPORES

The secondary uredospores of *Phragmidium potentillae canadensis* are especially interesting because of their general resemblance to the primary uredospores which arise from a fusion cell as I have described (6). The secondary uredospores also arise from a large basal cell which contains two large nuclei. The basal cell here is borne upon a mycelium of binucleated cells (fig. 1). No fusion occurs in its formation, but it is plainly the equivalent, in its mature condition, of the so-called "basidium" of the aecidium cup which arises from a fusion cell. The two nuclei of the basal cell divide by conjugate division, and the pair of daughter nuclei lying in the distal portion of the basal cell are separated off by a cross wall, thus forming the first spore-initial cell. A further conjugate nuclear division, followed by a cell division, at once separates this initial cell into a spore and a smaller cell below, which elongates to form a stalk upon which the spore is borne (fig. 2). About the time the first spore is formed, a bud appears on the basal cell beside the stalk of the first uredospore (fig. 3). A second simultaneous division of the nuclei of the basal cell provides this bud with two nuclei, leaving two in the basal cell. A wall now separates off this second uredospore-initial cell (fig. 4). It in turn divides, forming a second spore and stalk in the manner described for the first (fig. 5). In the same manner a third spore is produced (fig. 21).

On comparing these figures with the ones given in my description of spore-formation in the primary uredo (6) of this same rust, the striking likeness is at once apparent. The only difference lies

in the method of formation of the basal cells and in the binucleated condition of the vegetative mycelial cells from which they arise. The primary uredosorus arises from a mycelium of uninucleated cells (fig. 6), while the secondary uredosorus arises on a mycelium with regularly binucleated cells (fig. 1; compare figs. 19 and 21).

Like the secondary uredospores of *Phragmidium potentillae canadensis*, the uredospores of the Coleosporiums are borne upon a mycelium of binucleated cells. On this mycelium large basal cells are formed in the same way as in *Phragmidium*. When the spores form, however, as figured and described by HOLDEN and HARPER (4), the second uredospore-initial cell is cut off directly beneath the first spore and intercalary cell. This is repeated in the case of the following spores, and a row of uredospores separated by intercalary cells is formed, having exactly the appearance of the rows in the true aecidium (fig. 20).

Uredospores are generally unicellular, but, as ROZE (24) and later JACKY (15) have shown, the uredospores of *Puccinia chrysanthemi* are quite commonly two-celled.

TELEUTOSPORES

I have studied in detail the formation of the teleutospores of *Puccinia podophylli* S., and a similar series of cell phenomena to those described for the secondary uredospore of *Phragmidium potentillae canadensis* is to be observed here. A series of large binucleated cells is formed beneath the epidermis of the host. These cells are the ends of hyphae which are made up entirely of binucleated cells and are in position and general appearance exactly like the basal cells of the uredosori, and like those cells bear the spores. Conjugate nuclear division followed by cell division now separates off a large distal cell or teleutospore-initial cell (fig. 7). As in the case of the uredospore, this cell now divides to form the spore and the stalk (fig. 8). In the genus *Uromyces* the teleutospore remains unicellular. Here, however, like the uredospore of *Puccinia chrysanthemi*, this one cell divides to form the characteristic two-celled spore of the genus *Puccinia*. As is well known in *Triphragmium* and *Phragmidium*, three and four-celled spores are produced from a single initial spore-cell. It is plain that this multiplication of cells in the

teleutospore increases the number of sporidia produced and so increases the chances of infecting the aecidium host the following spring. The developmental stages in this case were worked out in greater detail in connection with the formation of the second spore produced from the basal cell. About the time the cell division for the formation of the first spore is complete, a hyphal bud is pushed up beside the stalk of the first spore. A nuclear division occurs in the region of the neck of this bud (fig. 9). The spindles are here so placed that there can be no question but that a daughter nucleus from each of the nuclei of the basal cell will enter the bud, while the other two daughter nuclei will remain in the basal cell. The bud is separated from the basal cell by a wall, thus forming the second teleutospore-initial cell. A simultaneous nuclear division follows within this cell (fig. 10), and a cell wall cuts off the spore cell and the stalk cell. That it is the upper one of these two cells which produces the two cells of the teleutospore is shown in fig. 11, where the cell wall is just forming. A third bud is formed at about this time and a third spore is produced in the same manner as has just been described (fig. 12).

While at work on the teleuto stage of *Puccinia podophylli* a further interesting phenomenon was observed. The occasional occurrence of trinucleated cells, together with BLACKMAN's account of migrations of nuclei among vegetative cells in *Puccinia poarum*, suggested that possibly nuclear migrations occur in the fungi, as well as in the higher plants, as purely pathological phenomena.

MIEHE (19) has shown that when the epidermis is stripped from the leaves of *Allium nutans* the nuclei of certain cells become pointed and finally a thin beak penetrates the wall into a neighboring cell. The portion of the nucleus which has passed the wall enlarges to form a highly refractive, densely staining vesicle. This vesicle increases in size as the nuclear material finally passes over into the foreign cell. MIEHE has found cells containing as many as five nuclei as a result of such migration. The explanation given is that the condition is a pathological one in which the nuclei migrate as a reaction to the wound inflicted in removing the epidermis.

SCHÜRHoff (26) found essentially the same phenomena occurring in *Iris germanica*. He also mentions the formation of the vesicle which has a marked affinity for the red of the triple stain.

A careful study of the teleutosori of *Puccinia podophylli* revealed that nuclear migrations are quite common here. This was particularly true at the base of the spores and in the margins of the sori. The nucleus forms a beak which penetrates into a neighboring cell (fig. 13). This projection elongates, forming a sort of thread as the material of the nucleus passes over into the foreign cell (fig. 14). At this stage the elongated portion of the nucleus loses its normal structure and becomes densely stained with the red of the triple stain. This dense staining is figured by MIEHE and SCHÜRHOFF, and appears in figures by BLACKMAN. The portion of the nucleus which has passed the wall now begins to enlarge (figs. 15, 16). In the latter figure there is evidence that the nucleus migrates from one cell of a hypha to the next, while in the other cases the nuclei appear to be migrating from one hypha to another.

Sections which show all the nuclei of the cells concerned in the migration are hard to obtain. By studying the series of sections to which fig. 14 belongs, it was found that cell *a* contained two nuclei, while cell *b* contained but one. From this it seems plain that in this case there is a migration between normal vegetative cells of the sporophyte where no fertilization can be assumed. This would result in the production of a cell with three nuclei. Indeed this condition is quite common (fig. 17).

The only interpretation possible here seems to be the one given by MIEHE, that this condition is entirely pathological and possibly due to the wound produced at the time of fixation. The fact that three- and four-nucleated spores are often found has been pointed out by SAPPIN-TROUFFY and BLACKMAN. If such spores result from pathological nuclear migration, this would indicate that the pathological condition which produced the migration must have occurred a considerable time before fixation, which is hardly an adequate hypothesis. The wounding in preparation for the killing solution perhaps explains well enough figures in which the nuclei are in process of migration. The fact that the migrations were observed in many cases in a sort of rudimentary paraphysis bounding the pustules is perhaps significant. It undoubtedly helps to explain certain conditions in the cuplike aecidia where isolated binucleated cells are often found in the older pustules quite out of range of the bases of the rows of spores where the fertilization processes occur.

MORPHOLOGICAL DISCUSSION

It cannot be decided, perhaps, on the data at present available whether the fusion at the end of the uninucleated generation is of a primary or secondary nature and origin. There can be no question, however, that it is physiologically the fertilization stage in the development of the rust, and that it is the beginning of a sporophyte generation which ends with the reduction divisions in the germinating teleutospore, as described by MAIRE (16, 17) and later by BLACKMAN (2). HARPER (13) has also argued, on the data given by BLACKMAN and myself, that an essentially similar alternation of generations is found in the rusts to that in the ascomycetes and red algae. The existence of well-defined gametophyte and sporophyte stages in these forms can no longer be questioned.

If we take up the cases of the aecidio-, uredo-, and teleutospores in the light of the facts above described, it is plain that we have in the successive production of these forms a series of asexual reproductive cycles within the sporophyte generation. In thus showing a series of subgenerations, each ending with a particular spore form, which taken together compose the sporophyte, the rusts are unlike any other group of plants in which true alternation of generations is known.

The essential characteristics of these subgenerations is that in each case they begin and close with the peculiar structure first described and long known as "basidium," or, as BLACKMAN has pointed out, better called the basal cell. This is the morphological unit, whose correct interpretation gives the key to the explanation of the puzzling and hitherto unexplained reduplication of forms which is at once the most conspicuous and least understood feature of the entire group.

With the establishment of the identity of the basal cells of the uredosori and teleutosori with one another and with the basidium of the aecidium, and the interpretation of this cell in the aecidium as the primitive spore-producing cell of the sporophyte generation of the rusts, the morphology of such diverse and puzzling structures as aecidio-, uredo-, and teleutospores and stalk and intercalary cells becomes at once clear.

Considered from this point of view, we find the gametophyte generation consisting of a mycelium of uninucleated cells, beginning

with the sporidia and ending with the fusion of two gametes, and bearing asexually one kind of spores, the so-called spermatia. The question as to how the so-called secondary aecidia arise must be regarded as still unsettled. DIETEL (11) has shown that infections from aecidia in the case of *Uromyces scrophulariae* DC. may reproduce crops of aecidiospores. In this case one or more of three things may have taken place: the infecting aecidiospore may have germinated by the formation of a sort of promycelium and sporidium, thus returning to the uninucleated condition, as is the case in *Endophyllum*; or these secondary aecidia may be borne upon a mycelium of binucleated cells, in which case they are not aecidia at all, but rather uredospores borne in rows such as occur in *Coleosporium*; or spermatia capable of producing infection may accompany some of these forms having the secondary aecidia.

Against this last view we have the present belief that the spermatia are functionless, a belief which in view of the great number of forms to be studied is certainly open to some question, especially since BREFELD (4) and PLOWRIGHT (20) claim to have seen distinct evidences of normal germination in the spermatia of *Puccinia graminis*, *Uromyces pisi*, *Puccinia tragopogonis*, *Puccinia coronata*, and others. This is a behavior quite unlike what might be expected of true spermatia. In my opinion, the likeness of the rusts to the red algae is very questionable, and the arguments that the spermatia are the former male cells are none too convincing. I incline rather to the view that spermatia represent the once functional asexual spores of the gametophyte. This view finds support in the fact that they are in general appearance very like the functional asexual spores (pycnidia) of the gametophyte of certain ascomycetes; also in structure and general appearance they are very like the other gametophytic spores of the rusts, the sporidia, which are still functional; further, unless we interpret the spermatia as the asexually produced gametophytic spores, the gametophyte generation is left entirely without means of reproducing itself without passing through the stages of the sporophytic generation. As yet, however, it must be admitted that definite evidence as to the nature of the spermatia is very incomplete.

The binucleated sporophytic generation which, as MAIRE (17) has pointed out, is comparable to the generation with the double

number of chromosomes in the higher plants, has its beginning in the cell produced by the fusion of two gametes—the fusion cell. This cell produces a more or less elongated outgrowth which has been long known as the "basidium," and has been often figured and fully described. For obvious reasons, that BLACKMAN has pointed out, the term basal cell is to be preferred to the old term basidium. This cell now produces spores, being a generative cell. The spores may be borne in chains, as has been so often described for the true aecidia, or they may be produced by a process of budding and so be borne on stalks, as I found to be the case in the primary uredosori (*figs. 18, 19*).

The spores produced by this first basal cell may infect the same host upon which the gametophyte is parasitic, or they may infect some other host and produce there a sporophyte mycelium. After a period of development this mycelium fruits. When spores are to be produced, large binucleated cells—the basal cells—in all essentials like the cells upon which the aecidiospores and primary uredospores are borne, again appear, this time upon the ends of the binucleated hyphae which mass together beneath the epidermis to form the uredosorus. By a process of cell division above described the uredospores are formed. These uredospores may be borne in rows and separated by intercalary cells, as in the case of *Coleosporium*, or they may be borne upon stalks, as described above for *Phragmidium potentillae canadensis*. The uredospores may reinfect the same host or hosts and repeat this generation an almost indefinite number of times, as is commonly supposed to be the case in *Puccinia rubigo-vera*.

Usually, after a few generations of uredospores have been produced, the binucleated mycelium bears the teleutospores which are to end the sporophytic phase in the life-cycle. When teleutospores are about to form, end cells of the hyphae again return to the condition of the large basal cell, and the teleutospores are budded off exactly as are the primary and secondary uredospores. At present we know of only one form in which the teleutospores are borne in chains and separated by intercalary cells. Another approach to this condition is perhaps found in the sessile teleutospore of *Melampsora* and *Coleosporium*. The teleutospores of the different genera are only secondarily characterized by being made up of one to several cells.

The bearing of these facts upon the problems of classification

presented by the rusts is of primary importance. Assuming the existence of alternation of generations, there can be no doubt that the gametophyte is to be regarded as the primitive, original generation. The autoecious rusts are probably to be regarded also as more primitive than those which are heteroecious. It is most suggestive of the truth of this view that the rusts show alternation of generations at the time the change from one host to another occurs. Older schemes of classification of course have left all such considerations out of account.

SCHROETER has classified the rusts on the ground of the various types of spores occurring in the life-histories of the different forms. To him we are indebted for the convenient separation into *eu*-, *-opsis*, *brachy*-, *hemi*-, *micro*-, and *lepto*- types. Obvious difficulties arise with this classification as used up to the present time. Assuming all primary uredospores to be in reality aecidiospores, as is the case in *Phragmidium potentillae canadensis*, would at once throw all of the *brachy*- and *hemi*- forms into the *Eupuccinia* class. If we retain the term *Brachypuccinia* on the ground of the primary uredospores having stalks, to be consistent it would be necessary to class *Coleosporium* with the *-opsis* forms, since its uredospores are borne in rows as are aecidiospores.

DEBARY (10) made his first division in the group by separating the aecidium-forming rusts from the so-called tremelloid forms. He regards the former as being homologous in essential details with the ascomycetes, and points out that the tremelloid forms may be regarded as either more primitive and in process of being developed, or reduced forms produced by the modification of the aecidium-bearing forms. It is plain, however, that with our present knowledge no such division is to be considered. As I have pointed out, the primary uredo is morphologically an aecidium. Further, Dr. OLIVE permits me to quote results, not yet published, which show that the teleutospores of *Puccinia transformans*, a *micro*- form, are borne upon basal cells which are the outgrowth of a fusion cell produced upon a mycelium having uninucleated cells. There are then teleutospores which in their origin are the same as the aecidiospores and primary uredospores, and this argues very strongly that the stage with uninucleated cells is to be regarded as always present.

ARTHUR'S (1) new classification is based upon the assumption that all of the spore forms—*spermatia*, *aecidio-*, *uredo-*, and *teleutospores*, and *sporidia*—were present in the ancestors of our rusts, and he leaves untouched the question of the origin of this multiplicity of spore forms. Reasoning from this assumption, the forms with abbreviated life-cycles arise by a process of elimination. In this way any portions of the sporophyte and perhaps the whole gametophyte might be successively suppressed.

Endophyllum has perhaps arisen in this way. In it a uninucleated mycelium produces binucleated aecidiospores which apparently have no uredo host. The spores germinate by a sort of promycelium which bears four uninucleated sporidia. These sporidia again infect the aecidial host, producing again a mycelium of uninucleated cells.

If we assume on the other hand that the rusts evolved from lower fungi, and that the various subgenerations of the sporophyte are being added and intercalated, as well as perhaps in some way old forms eliminated, quite a different classification is suggested. The gametophyte is universally regarded as the primitive generation, and in its earliest appearance was relatively simple. In the pteridophytes the sporophyte increases in importance until the gametophyte is finally the more inconspicuous.

I incline to the view that the *lepto-* and *micro-* forms, in which the teleutospores or spermatia and teleutospores only occur and are borne on mycelia with uninucleate cells, are the primitive rusts. We have in them the gametophyte bearing the gametes and producing the fusion cell. A very short outgrowth of this cell now bears the teleutospores in which the sporophyte generation has its end. The first modification of this life-history would then appear in a further development of the sporophyte. This might be brought about by the fusion cell producing a mycelium directly rather than the basal cell normally produced, or it is possible that the basal cell should produce temporary spores, which might carry this sporophytic mycelium to other tissue, a result which would be altogether favorable on account of the exhausted condition of the host in the neighborhood of the fusion cell. Spores formed in this way would conform to our definition of primary uredospores, which it would thus appear are to be considered as the first added spore generation, and the *brachy-* form would thus be the first

derived type. With such a first crop of temporary spores once formed, it is easy to see how they might be formed in successive crops—the secondary uredospores—before the teleutospores are finally formed and the sporophytic generation closed.

A modification of the stalk cell with loss of essential function would result in the formation of the true aecidium. The short intercalary cells of the aecidium give us a decided argument for the belief that the aecidiospores are not the primitive spore type, since I am of the opinion that we can only regard the intercalary cell as practically a functionless cell. The argument that the intercalary cell is for the purpose of disjoining the spores is hardly tenable, since we have many fungi in which, as in *Cystopus*, chains of conidia are formed, the spores of which separate readily without alternating sterile cells. Looked upon as a rudimentary stalk, we can hardly assume that it is in process of progressive evolution, since from that point of view we would have the curious case of a functionless structure being first developed, to be modified later into a structure of some service to the plant. It is relatively common, on the other hand, to find that functional structures degenerate on becoming useless, becoming smaller and finally disappearing. The degeneration of the uredo stalk cell is doubtless correlated with the development of the spore pustule, resulting in the formation of the spores in chains instead of in a horizontal series. The spore-initial cells, which have in other cases divided to produce spores and stalk cells, still divide, forming the spore and the small intercalary cell, the degenerated representative of the former stalk cell. With the change from the stalked primary uredospores to the chains of aecidiospores, we have formed the typical autoecious *eu-* type of rust. If now the sporidia find a more favorable host in some other plant than that bearing the uredospores and teleutospores, a later change of host for the sporophyte generation would explain heteroecism. It is certainly conceivable that the change of host should occur at the germination of the first-formed binucleated spore. Certainly the sporidia and the gametophytic mycelia produced by them are sufficiently different from the sporophytic aecidiospores and uredospores and the mycelia which they produce to explain such a change in some measure.

From either point of view it would appear that a heteroecious

eu- form is the highest in complexity and a late stage in the development of the rusts. The peridium is undoubtedly a late modification for protection, and cuplike aecidia are very likely less primitive than the cæomas. This would argue that a rust of the *Puccinia graminis* type is in structure very far removed from the primitive rust, a view which is quite opposed to the stand taken by BLACKMAN.

I entirely agree with DIETEL (12) that the presence or absence of the secondary uredospores in the life-cycle is of secondary importance when considering the history of the rusts. The essential stages are those of cell fusion and chromatin fusion and reduction. The uredospores simply prolong the sporophytic phase as the conditions demand, and it is likely that the *-opsis* forms may result from the elimination of the uredo stage in some rusts; while in others they represent an earlier less complete stage in evolution than the *eu-* forms.

The curious condition found in *Endophyllum* may well have arisen by the elimination, for some cause, of the teleuto and uredo stages. The cuplike structure and short intercalary cells all point to its once having been a very highly specialized form from the standpoint of evolution. It is quite conceivable that as a result of some change in condition the aecidiospores should have developed the capacity to reinfect the aecidium host.

The facts of alternation of generations in the rusts are in harmony with DIETEL's view that the *micro-* and *lepto-* forms are the most primitive types of rusts. Besides the arguments advanced above, we have in the diverse structures of the teleutospores of the different genera a further support for this view. Assuming the teleutospores to be the oldest spore form, it is easy to see how they might have become more markedly modified than the newer uredo- and aecidiospores. The loss of function of the spermatia as gametophytic conidia, too, is exactly what might be expected with the development of the sporophytic spores.

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EXPLANATION OF PLATE VII

Figs. 1-17 were drawn with the camera lucida, using ocular IV and the $\frac{1}{16}$ oil immersion objective of Leitz. *Figs. 18-22* are semi-diagrammatic and the magnification has been adjusted to bring the figures of the different rusts to approximately the same dimensions on the plate.

Phragmidium potentillae canadensis

FIG. 1.—A portion of the mycelium showing the binucleated condition of the cells of the secondary uredo.

FIG. 2.—The first spore-initial cell dividing into spore and stalk cell.

FIG. 3.—An early stage in the budding-off of the second spore.

FIG. 4.—A fully formed second spore-initial cell.

FIG. 5.—The divisions forming the second spore and stalk have been completed; the stalk of the first spore is also shown.

FIG. 6.—A portion of the mycelium showing the uninucleated condition of the cells (compare with *fig. 1*).

Puccinia podophylli

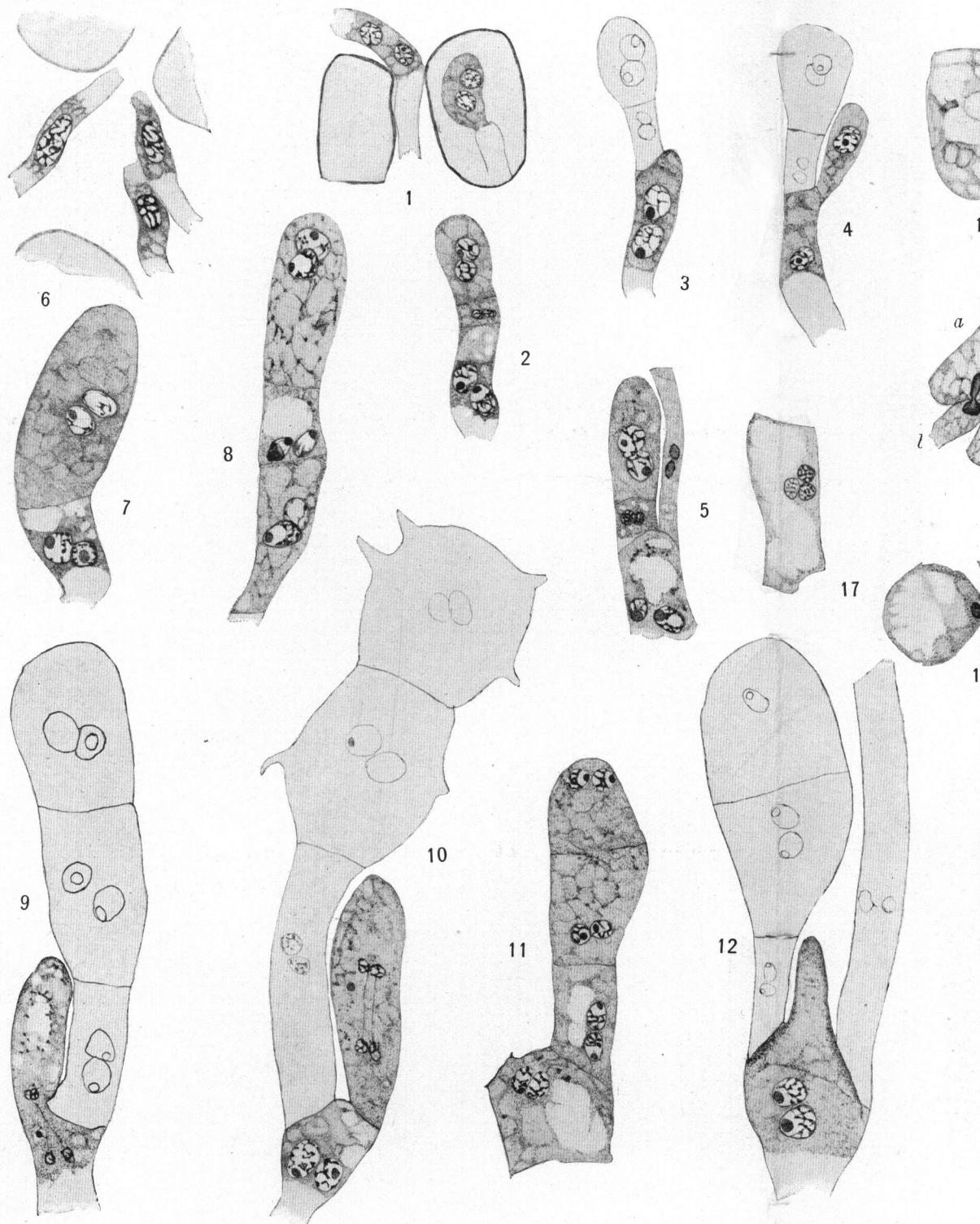
FIG. 7.—A stage showing the basal cell and the first teleutospore-initial cell.

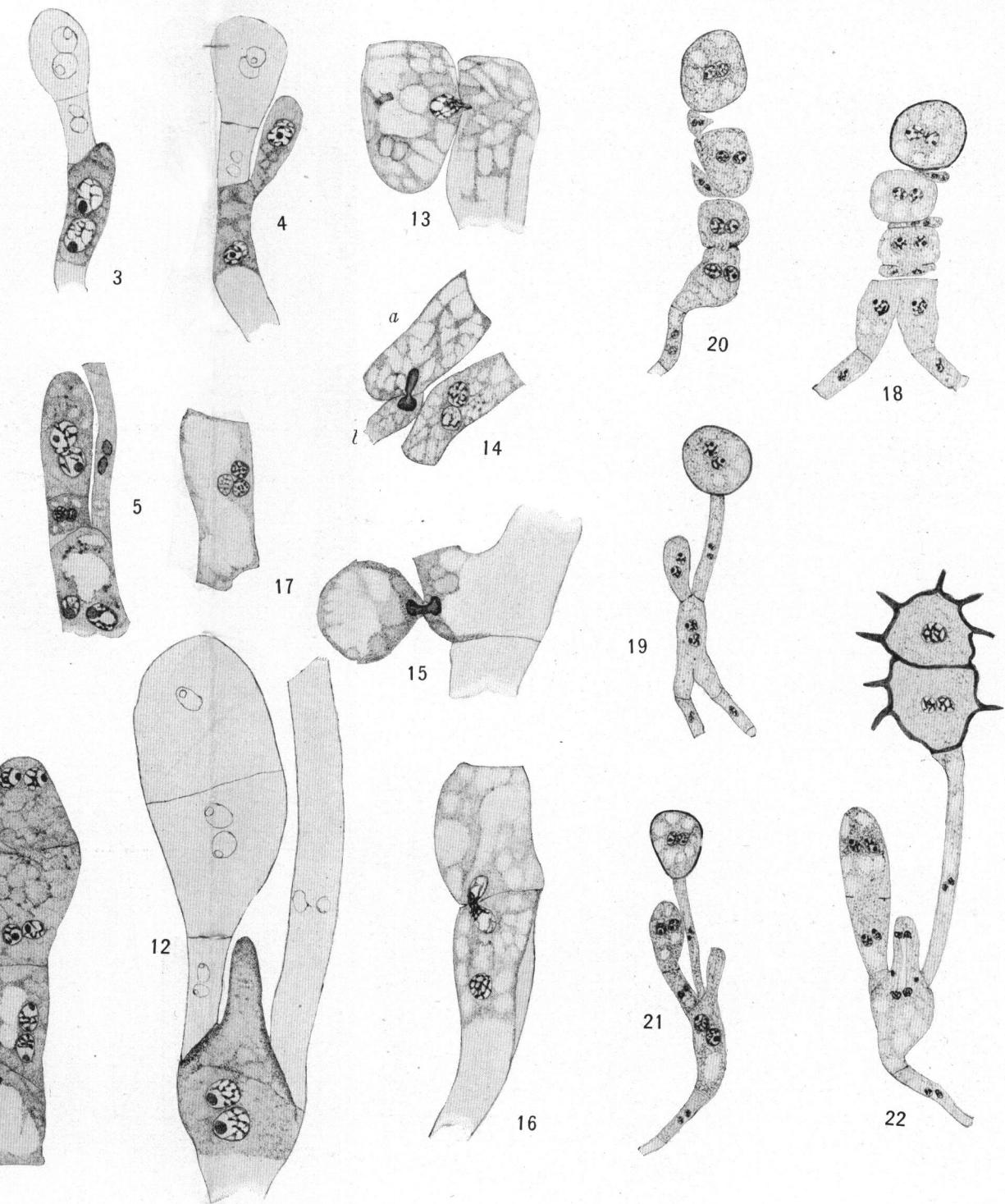
FIG. 8.—The spore-initial cell has divided into a stalk cell and a larger distal cell which is to divide and produce the two-celled teleutospore (see *fig. 11*).

FIG. 9.—Simultaneous nuclear division supplying the second spore-initial cell with nuclei.

FIG. 10.—A second spore-initial cell showing nuclear division before division into stalk and spore.

FIG. 12.—A stage showing the division of the distal cell into the two cells the spore.





FIGS. 13-16.—Various stages of nuclear migration in the mycelium of the teleutosorus.

FIG. 17.—A mycelial cell showing three nuclei.

Semi-diagrammatic figures

FIG. 18.—*Phragmidium speciosum*. Mycelial cells of the aecidium showing uninucleated cells bearing a fusion cell and the rows of spores and intercalary cells.

FIG. 19.—*Phragmidium potentillae canadensis*, showing uninucleated mycelial cells in the primary uredo similar to those in the aecidium; a fusion cell is formed in much the same way as in the aecidium; the elongated basal cell represents an outgrowth after fusion; here the spores are budded off as a horizontal series and are borne on stalks.

FIG. 20.—*Coleosporium solidaginis*. Uredospores borne in chains on a mycelium of binucleated cells.

FIG. 21.—*Phragmidium potentillae canadensis*. Secondary uredospores budded from the basal cell; the mycelium is composed of binucleated cells.

FIG. 22.—*Puccinia podophylli*. Teleutospores in various stages of formation; the cells of the mycelium each contain two nuclei.